But what if it wains??

INDIRECT INTERACTIONS BETWEEN THE INVASIVE BROWN SPRUCE LONGHORN BEETLE, *TETROPIUM FUSCUM*, AND A NATIVE DEFOLIATOR, *CHORISTONEURA FUMIFERANA*

by

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ABSTRACT

Two important pests in Atlantic Canada are an invasive beetle, the brown spruce longhorn beetle (BSLB), and a native defoliator, the spruce budworm. Both species are currently attacking spruce in separate regions; however, there is a high likelihood that these attack ranges will overlap. It remains unknown what impact concurrent attacks of these herbivores might have on trees, or on population trends for either species. We investigated the effects of BSLB on interactions between spruce budworm and red spruce, using field experiments near Halifax, Nova Scotia. We established four stress treatments involving natural and simulated BSLB attack, with five branches on each tree assigned densities of spruce budworm. We measured the impact of natural and simulated BSLB attack on red spruce, and spruce budworm defoliation and examined its dependence on budworm density. We also examined performance of adult moths through fecundity measurements. Natural and simulated BSLB attack did not change density-defoliation relationships, relative to no attack. Survival of spruce budworm on red spruce appeared to be reduced as spruce budworm density, presumably due to reductions in the availability of the preferred developing foliage. There are indications that, in general, simulated BSLB stressed trees allow higher larval survival than trees with natural BSLB attack or trees that are unattacked.

DEDICATION

To the budworm, without you, none of this would have been possible.

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CHAPTER 1 - GENERAL INTRODUCTION

MALLORY MACDONNELL

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Insect herbivores can have a negative influence on plant growth and development, particularly when they outbreak or establish on novel hosts. Insects that occupy different niches can have different impacts on the host depending on what part of the plant they consume. For example, defoliating insects on trees inflict damage by the removal of leaf tissue (Sanders 1995), whereas the consumption of phloem by phloem-feeding beetles disrupts the transport of water and nutrients between roots and foliage (Juutinen 1955). Defoliators and phloem-feeders do not compete directly for the same plant tissues, although they can nevertheless interact indirectly, since when trees are under attack, resources are reallocated (Alder et al. 2001). Such interactions are of interest partly because they can influence the population dynamics of both insect species, but also because they are likely to impact the severity of herbivory on the tree (eg. Annila et al. 1999, Wallin and Raffa 1999, Colgan and Erbilgin 2011).

A potentially important example of host-mediated interactions involves the outbreak defoliator spruce budworm (*Choristoneura fumiferana* Clem.) and the phloem-feeding brown spruce longhorn beetle (*Tetropium fuscum* Fabricius). Currently both are important pests of spruce (*Picea* spp.) in Atlantic Canada. The spruce budworm is a native outbreaking moth of the boreal, Great Lakes, and Acadian forest in Canada and the northern U.S.A. An outbreak is currently occurring in Quebec, originally established on the north shore of the St. Lawrence River, and is expected to soon spread through Atlantic Canada (Blais 1983, pers. comm. Rob Johns 2017, NRCAN). The larval stage damages conifers through feeding on the current-year foliage (Miller 1977; Sanders 1991), and sometimes older foliage, depending on food availability and the synchrony between the insect and the host tree. An accumulation of defoliation over several consecutive years can weaken trees, leading to growth loss and mortality, and increased susceptibility to secondary insects and diseases (Sanders 1995). Concurrent with this outbreak, spruce stands in Nova Scotia are experiencing an invasion of a European brown spruce longhorn beetle. This beetle is believed to have arrived in Halifax in the early 1990's (Smith and Hurley 2000) and has since been under regulatory control by the Canadian Food Inspection Agency. In Nova Scotia, the beetle attacks mainly stressed red spruce trees, with the larvae inflicting the majority of the damage after they bore into the trunk to feed on the phloem. The resulting network of feeding galleries can girdle the tree, cutting off water and nutrient supply, thereby killing the tree (Juutinen 1955). BSLB was first discovered at Point Pleasant Park, next to a shipping port, in Halifax (Smith and Hurley 2000), and has since spread to more counties across Nova Scotia. There have been individual BSLB detections in New Brunswick throughout the last 5 years, but the population is still not considered established (pers. comm. Jon Sweeney 2017). This suggests that the invasion range is gradually spreading northwest, and populations may establish in New Brunswick in the near future. This could likely result in a range overlap between spruce budworm and BSLB.

We know a great deal about how spruce budworm impacts spruce growth and survival (Miller 1977; Bauce et al. 1994; Lawrence et al. 1997), and about how budworm interacts with its predators and parasites (Miller 1959; Jennings and Crawford 1989; Régnière and Nealis 2007), but we know little about how it interacts with other co-occurring herbivores. In particular, the indirect interactions between BSLBand spruce budworm are novel (since the beetle is non-indigenous) and potentially important (since each insect has major impacts on spruce). In this thesis, I explore some of the applied and ecological aspects of interactions between brown spruce longhorn beetle damage on spruce budworm.

My overall goal was to investigate the effects of BSLB damage on interactions between spruce budworm and its host. I approached this question through field experiments that focused on two main objectives. The first was to determine the effects of beetle attack on relationships between spruce budworm density and associated defoliation. The second was to assess the effects of BSLB feeding (and tree stress) on spruce budworm performance. The specific objectives addressed in Chapter 2 and Chapter 3 are outlined below.

We hypothesized that the effects of simulated and natural BSLB attack would increase (steeper slopes) spruce budworm density-defoliation relationships. The re-allocation of resources from beetle attack throughout the host would cause an increase in defoliation per unit of budworm. Our second hypothesis was that through similar mechanisms, spruce budworm performance would be significantly decreased due to simulated and natural BSLB attack. We used sleeve cage experiments on trees receiving simulated and natural BSLB-attack stress, since these strategies have been used previously to ask similar questions in this and other plant-insect systems. We were able to test our predictions, and also to examine another question about the effects of high spruce budworm larval densities and intraspecific competition on density-defoliation relationships. These density-defoliation relationships have interesting implications for spruce budworm population dynamics when examining high densities on red spruce.

about density-defoliation relationships at very high larval densities. The latter question has interesting implications for spruce budworm population dynamics.

In Chapter 2, we investigate the effects of simulated and natural BSLB attack and spruce budworm larval density on density-defoliation relationships for spruce budworm on red spruce. Trees subjected to stress had significantly more current-year shoot production, but smaller shoots. Overall defoliation increased with larval density in both years. There was no significant difference in defoliation between stress treatments in either 2014 or 2015. Chapter 3 examined the effects of simulated and natural BSLB attack and spruce budworm larval density on spruce budworm adult performance on red spruce. Performance was measured using fecundity (wing length) and survival. In both seasons, there was a negative effect of budworm density on budworm survival, but no effect of beetle attack on budworm survival. In 2014, there were effects of budworm density and beetle attack on forewing length of spruce budworm adults, but not in 2015.

As the author of this thesis, I wrote the manuscript, experimental design, conducted experiments, and conducted data analysis. The two co-authors listed (Dr. Stephen Heard and Dr. Rob Johns) both aided with experimental design, data analysis, and revisions of the manuscript.

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CHAPTER 2 - DENSITY-DEFOLIATION RELATIONSHIPS FOR SPRUCE BUDWORM ON RED SPRUCE: EFFECTS OF GIRDLING STRESS, WOOD-BORING BEETLE ATTACK, AND HIGH BUDWORM DENSITY

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ABSTRACT

Two important forest pests in eastern Canada are an invasive wood-boring beetle, the brown spruce longhorn beetle (BSLB, *Tetropium fuscum* Kirby), and a native defoliator, the spruce budworm (*Choristoneura fumiferana* Clem.). Conifer forests in Eastern Canada are currently under attack by both species, albeit in separate regions. However, there is a high likelihood that these two attack ranges will overlap within the next decade. It remains unknown what impact concurrent attacks of these herbivores might have on trees or population dynamics of either species. We investigated the effects of BSLB on interactions between spruce budworm and red spruce (*Picea rubens* Sarg.), using field experiments on red spruce near Halifax, Nova Scotia. We had two main objectives to examine the impact of BSLB attack: 1) to examine how BSLB attack affects red spruce growth, and 2) to elucidate larval density-defoliation relationships for budworm on red spruce that had been subjected to different levels of stem damage (either through girdling or BSLB attack). We exposed trees to four different stress treatments, including natural and simulated BSLB attack (control, BSLB attack in exclusion cages, girdling, and girdling plus BSLB attack). Five branches on each tree were assigned densities of spruce budworm of 0, 10, 20, and 40 fourth-instar larvae in 2014 and 0, 30, 90, and 120 second-instar larvae in 2015. We measured defoliation and examined its dependence on budworm density. Trees subjected to stress had significantly more current-year shoot production, but smaller shoots. Overall defoliation increased with larval density in both years. There was no significant difference in defoliation between the four stress treatments in either 2014 or 2015. But there was a significant difference in defoliation relationships between spruce budworm larvae densities. Fourth instar larvae defoliation in 2014 plateaued, where density-defoliation relationships no longer show increasing damage despite increasing larval densities, at approximately 0.5 larvae per shoot, at 100%, 60%, and 20% for current-year, one-year old, two-year old respectively. For all foliage together, the plateau was at 40% defoliation. Second instar larvae defoliation in 2015 plateaued at approximately 1 larvae per shoot at 100% and 40% for current-year and average total branch shoots, and defoliation peaked at approximately 4 larvae per shoot at 60% and 40% for one-year old and two-year old shoots respectively. These relationships will provide insight into the potential impacts of these two insects if or when their population ranges coincide, while the density-defoliation relationships of spruce budworm may aid in decision-making practices for management.

INTRODUCTION

Herbaceous insects in general can often have a negative influence on plant growth and development (Zlotin and Khodashova 1980; Coulson and Witter 1984; MacLean 1984; Alfaro and Shepherd 1991). The magnitude and type of damage an insect causes, however, varies dramatically depending on what plant tissue is being exploited. Defoliating insects, for instance, consume the photosynthetic tissues of their host, which in effect removes the primary tissues needed to generate carbohydrates for growth and defense (Sanders 1995, Underwood 2010). Wood-boring beetles, in contrast, consume phloem tissues in the stem, and at high densities can cut off the movement of water and photosynthate between the tree crown and roots (Juutinen 1955). Owing to their significant economic and ecological impacts, both defoliators and bark beetles have been studied extensively, though usually independently. Several studies to date have examined how these different guilds might indirectly affect one another's success and impact when their attacks co-occur in the same spatial region. Most of these studies examine the impact of defoliators on bark-beetles (eg. Colgan and Erbilgin 2011, Wallin and Raffa 1999, Annila et al. 1999), where tree-resistance to beetle attack was decreased from defoliation.

In eastern Canada, coniferous forests are susceptible to attacks by many insect species. Two major species in Eastern Canada, in their respective ranges, are the brown spruce longhorn beetle (BSLB, *Tetropium fuscum* Kirby) and spruce budworm (*Choristoneura fumiferana* Clem.). BSLB is an invasive beetle from Europe and was first detected in stands of red spruce (*Picea rubens* Sarg.) around the Halifax port area in the 1990's (Smith and Hurley 2000). It has since continued to expand north and was first detected in southern New Brunswick in 2014, in Memramcook (CFIA 2014). BSLB adults lay eggs under bark scales and the larvae create galleries in the stem phloem (Juutinen 1955). After multiple generations of attack, the galleries sever the phloem tissues, and eventually kill the tree (Juutinen 1955). At the same time, a budworm outbreak has expanded to over 7 million hectares in southeastern Quebec as of 2016, and there are significant budworm populations in northern New Brunswick (NRCAN, Healthy Forest Partnership).

With BSLB moving north, and the budworm outbreak spreading south, these outbreaks may eventually overlap. While spruce budworm tends to prefer balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) it is also known to attack black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenburg) and red spruce, though there are fewer studies examining interactions between budworm and these latter, less favored species (Hennigar et al. 2008). Hennigar et al. (2008) showed a clear, consistent hierarchy of host species defoliation of spruce budworm, which is as follows. In a mixed stand, Hennigar et al. (2008) found that white spruce, red spruce, and black spruce defoliation was 72%, 43%, and 27% respectively, while balsam fir defoliation was 100%. The major difference in defoliation is due to differences in phenology of host buds and larval development timing (Greenbank 1963). White spruce buds burst on average only 4 days after balsam fir (but shoots develop faster than balsam fir (Swaine and Craighead 1924), while red spruce and black spruce burst about 13 days after balsam fir (Greenbank 1963). If the emergence of budworm from winter diapause is cued to availability of balsam fir, then other hosts are phenologically mismatched. Despite this lower susceptibility of red (and black) spruces, the importance of these trees in eastern forests (and the conservation status of red spruce) means that even limited defoliation may have important ecological and economic consequences. Red spruce is especially a concern in Nova Scotia where stress from BSLB and warming climates have the potential to exacerbate impacts of budworm once it reaches outbreak densities in the province (McLaughlin et al. 1986). As BSLB is a fairly new species to Canada, there is no information yet on how its attack might indirectly influence the success and impact of budworm on red spruce (or vice versa).

Relationships between the defoliator density and subsequent defoliation and damage of host trees are fundamental to integrated pest management. These relationships are particularly useful for decision-making around when to control forest pests in a typical foliage protection strategy through examining current and predicting future damage (e.g. Parsons et al. 2005, Johns et al. 2006, Pinault and Quiring 2008). In most instances, however, these relationships have been established in the absence of other pests, and it remains uncertain how these relationships might be altered by bark beetle feeding. Some defoliators can improve performance on stressed trees by increasing their foliage consumption as a way to compensate for reduced food quality, which would increase *per capita* defoliation (plant stress hypothesis: White 1984); however, other defoliators suffer reduced survival on stressed trees, which in turn could lead to reduced *per capita* defoliation (plant vigor hypothesis: Price 1991). Spruce budworm density-defoliation relationships have been developed for peak to declining populations on balsam fir and white spruce (Carter and Lavigne Annual Reports 1984-1993, Bauce et al. 2004, pers. comm. Alain Dupont 2017), but are unavailable for black and red spruce.

Here, we report field experiments where our overall goal was to investigate the effects of BSLB damage on interactions between spruce budworm and host, spruce. Our studies were carried out in Nova Scotia within the current BSLB invasion zone and used both natural (i.e., oviposition by caged BSLB adults) and artificial stress treatments (i.e., stem girdling) to simulate different intensities of bark beetle attack. This field experiment focused on two main objectives. First was to examine how the growth of red spruce that had been subjected to different levels of stem damage (either through girdling (simulated BSLB attack) or natural BSLB attack) was affected, and second was to elucidate the effects of stem damage on larval density-defoliation relationships for budworm on red spruce.

METHODS

Study Species Life History

Spruce budworm is the major pest of balsam fir and spruce throughout North America. Outbreaks of budworm occur in the spruce-fir forests at regular intervals averaging 30-40 years (Royama 1984). Since the mid 1980's, populations were nearly undetectable in Nova Scotia (NSDNR), even as the current outbreak began in Quebec and has been slowly spreading into New Brunswick (NRCAN). Spruce budworm is univoltine, and overwinter as second instar larvae. In Nova Scotia, larvae emerge in early May from their overwintering hibernacula and move toward the tips of branches in response to light (Miller 1963). Larvae can further disperse to nearby trees on wind currents using silk threads. Once larvae emerge from hibernation, they may mine one-year-old needles before dispersing to the current-year bud to form a feeding tunnel. Larvae develop through five to six instars with most of the feeding and damage occurring during the final instar (Miller 1976). Spruce budworm prefer young foliage, which generally has high levels of foliar nitrogen, phosphorous, potassium, copper, sugars, and water, also lower levels of foliar calcium, phenolics, and toughness (Lawrence et al. 1997; Carisey and Bauce 1997). When larvae are forced to consume older foliage, their performance suffers (Lawrence et al. 1997; Carisey and Bauce 1997).

Pupation often occurs near the feeding tunnel and the pupal stage lasts from 8 to 12 days from mid to late July. Adults live approximately 2 weeks, and oviposit in late July to early August. Females carry as many as 200 eggs and lay them in masses of approximately 20 eggs on the surface of needles (McGugan 1954, Morris 1955, Miller 1963). The egg stage lasts for 8 to 12 days and first-instar larval emergence occurs around mid-August (McGugan 1954, Stairs 1960, Miller 1963). Prior to overwintering, larvae do not feed, but can disperse by silk and wind to find an overwintering site where they spin a hibernaculum and moult to the second instar.

Adult BSLB are highly mobile and emergence begins in the spring and continues over a 6 to 8-week period. Both males and females are sexually mature upon emergence (Juutinen 1955), and thus mating and selection of host tree occurs almost immediately. Oviposition occurs three or four days after adult emergence. Females can lay between 28 and 108 eggs under bark scales or in crevices between scales. Eggs are laid in lines in singles or in pairs (Juutinen 1955). Larvae hatch after 10 to 14 days, then burrow into the trunk of the tree. Larval feeding creates galleries in the tree’s phloem, and larvae overwinter in the galleries. In the spring, larvae pupate and emerge as adults to mate and lay eggs (Juutinen 1955). After multiple generations of attack, connecting galleries can cut off the movement of photosynthate and water between the roots and the crown, leading to death of the host tree (Flaherty et al. 2013).

Red spruce is a shade tolerant conifer native to Eastern North America. Red spruce has a narrower distribution range than white or black spruce, and is a target of conservation due to widespread decline along the east coast of North America (Johnson 1987). It is the provincial tree of Nova Scotia, and is economically important as a commercial species for pulp and lumber. Red spruce buds flush later in season relative to other spruce species in Nova Scotia. Buds flush on average 9 days after white spruce, and on average 15 days after peak spruce budworm second instar larval emergence (Blum 1988). The more asynchronous larval and bud development, the greater budworm larval mortality and dispersal (Eidt and Cameron 1971). However, this cost of feeding on red spruce is offset to some degree because older red spruce needles are a more suitable source of nutrients compared to other spruces, and therefore more emerging larvae can survive until buds flush in the spring (Blum 1988).

Study area characteristics

We chose one field site in the BSLB range, in Sandy Lake, Hammonds Plains, Nova Scotia. Hammonds Plains is approximately 25 km from the suspected introduction point in Halifax. The study area is a mixed forest dominated by red spruce. Other common trees include balsam fir, red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh.), and white pine (*Pinus strobus* L.). Trees are open-growing, with moss covered rocky terrain. Different sections of the stand were used in 2014 and 2015.

Sleeve cage experiment

In 2014 and 2015, we haphazardly selected healthy, mature red spruce trees at least 5 m apart and lacking visible damage from BSLB (e.g. exit holes or resinosis) or feeding by defoliators (Table 1). In 2014, we used sixty trees divided among three treatments of 20 trees: control, girdled, and girdled plus BSLB attack. We placed mating pairs of BSLB in exclusion cages on the trunk of the trees for BSLB attack. Exclusion cages are fine-mesh sleeves used to prevent beetle from leaving the bole, but also predation of the beetles. In 2015, we used forty trees divided among four treatments: control, girdled, girdled plus BSLB attack, and BSLB attack only. We used girdling to simulate extreme BSLB attack, since multiple generations of repeated BSLB attack impede phloem conductance, as does girdling (Flaherty et al. 2011). In the spring of the treatment year, we used chainsaws to cut the trunk of each "girdled" treatment tree, approximately 15 cm from the ground (Figure 1) and to a depth of 1 cm to sever the phloem tissues. BSLB-treatment trees were exposed to one mating pair of BSLB, which were caged on the trunk at chest height at the end of May. To further increase beetle attack on BSLB-treatments, we hung pheromone lures (aPhinity BSLB: S-Fuscumol, from Sylvar Technologies) on the trunk at chest height, to attract local beetles.

We selected five mid-crown branches haphazardly from each tree before bud burst and measured from the terminal shoot to 45cm back on the branch. For each branch, we visually estimated percent defoliation on a shoot by shoot basis from the main axis and second order branches, using 0, 5, 10, 20, 40, 60, 80, 95, and 100% classifications (Figure 2) (Fettes 1950). Defoliation was measured before commencing the experiment to account for needle loss from environmental causes or other insect defoliators. We counted new developing buds on each branch and the terminal and distal lateral one-year old shoots were measured when branches were selected (Figure 2).

We obtained second-instar spruce budworm, overwintering on cheesecloth, from rearing facilities in Sault Saint Marie, Ontario (Insect production lab, Great Lakes Forestry Centre), in 2014 and 2015. In 2014, we reared the larvae under laboratory conditions from second instar until their fourth instar. Second instar larvae overwintering in cheesecloth were housed in beakers, which were covered in parafilm. Larvae were stored at room temperature (22 °C) and spritzed with water every day until emergence. Once emerged, larvae were placed on McMorran artificial diet (from the Insect production lab at the Great Lakes Forestry Centre) until fourth instar. The McMorran artificial diet consists of a mixture of agar, alphacel, ascorbic acid, aureomycin, casein, formaldehyde, linseed oil, methyl paraben, potassium hydroxide, sugar, vitamins, water, wheat germ, and wesson salt in ¾ oz clear cups with cardboard lids. Larvae were then placed on branches at bud burst (10 to 12 of June). In 2015, we placed second-instar larvae on cheese cloth in groups of 10 and we pinned the cheesecloth to the branch before bud burst (20 to 25 of May). In 2015, we used similar treatments but because we set up the experiment using younger larvae (second instar) we offset potentially higher larval mortality by tripling densities from the previous year's experiment (i.e. to 30, 60, and 120). This experiment was done using second instar larvae, rather than fourth instar as in 2014, since we were trying to get a better phenology match with the bud burst of red spruce.

To establish density-defoliation relationships on these different stress treatments, we placed pre-determined densities of budworm larvae on branches and enclosed them in fine mesh-cloth sleeve cages affixed to branches with twisties for the duration of development. We assigned a different spruce budworm density treatment to each branch. In 2014, these were: (1) control (no larvae or sleeve cage); (2) procedural control (no larvae, but fitted with a sleeve cage); (3) 10 fourth-instar larvae per branch with sleeve cage; (4) 20 larvae per branch with sleeve cage; and (5) 40 larvae per branch with sleeve cage. At the end of each field season, after all larvae had pupated, branches with cages were collected. Percent defoliation was visually estimated again after spruce budworm defoliation (Fettes 1954). Current-year shoots were counted, and terminal and distal lateral shoots were measured. We analyzed only defoliation that occurred during the experiment, by measuring defoliation before the experiment and subtracting it from final defoliation.

Statistical analyses

We used a one-way ANOVA to compare number of current-year, one-year old, and two-year old shoots among treatments and the length of current-year terminal lateral shoots for each of the two years. We then used Tukey's honest significant difference test to compare number of current-year shoots between treatments, and length of current-year terminal shoot lengths between treatments (R version 3.1.3). To compare number of shoots between treatments and length of shoots between treatments, only control and procedural control branches were used, to eliminate any effects of spruce budworm defoliation.

In 2014, the experimental design was a split plot (used to test for differences between two or more independent groups, while subjecting trees to repeated measures), and we used a mixed-factor analysis of co-variance to test for differences between treatments by looking at the differences in slopes, intercepts, and their interactions. We used three levels of treatment, which was one factor with three levels of stress (control, girdling, and girdling plus BSLB).

In 2015, a fourth stress treatment was added, girdling plus BSLB mating pairs, changing the design to a two by two factorial (girdling × BSLB). The analysis is otherwise unchanged from 2014.

Larval density treatments were standardized across all branches, by using the number of larvae per shoot. This procedure is appropriate because the selected branches differed in number of shoots, and therefore in resources available to feeding larvae.

We pooled the two treatments involving girdling, since there was no significant difference between density-defoliation relationships. We compared linear and nonlinear regressions for each group, then used Akaike information criteria to measure the relative quality of each model for each treatment to determine the best fit.

RESULTS

Overall spruce budworm larval survival in sleeve cages to pupation was 23% in 2014 and 10% in 2015. The procedural control had no impact on tree growth and development in 2014 or 2015 ($P < 0.05$) based on number of current-year shoots (Table 2). Trees subjected to girdling and girdling plus beetle attack treatments had an average of 50 more current-year shoot production in 2014 (Figure 3a), but no significant difference in number of shoots in 2015 (Figure 3b). In contrast, tree stress treatments reduced current-year terminal shoot length in 2014 by an average of 1 mm (Figure 3c), but there was no significant difference in shoot length in 2015 (Figure 3d).

There was minor (between of 0-5%) previous defoliation on current-year, one-year old, and two-year old shoots before larvae were placed on branches. This was removed from the average defoliation after spruce budworm attack. There was no significant difference in defoliation among stress treatments in either 2014 (Table 3) and 2015 (Table 4) with $P = 0.33$ and $P = 0.68$ respectively, therefore all girdled and BSLB only treatment data were pooled for further analysis. Density-defoliation relationships between age classes (current-year, one-year old, and two-year old) showed significantly different trends from one another. Based on delta AIC (Tables 5 and 6), non-linear fits outperform linear ones, with the sole exception of one-year old foliage in 2014, for which neither the non-linear nor linear fit was strongly favored. Overall defoliation increased with larval density in both years. Above densities of 0.5 fourth instar larvae per shoot in 2014 and one second instar larvae per shoot in 2015, densities were high enough to reach 100% defoliation of current-year foliage. For one-year old foliage, defoliation plateaued at 60% in 2014 (Figure 4) and peaked at 60% in 2015 (Figure 5). Two-year old foliage defoliation plateaued at 20% in 2014 (Figure 4) and peaked at 40% in 2015 (Figure 5), and total branch defoliation (average of current-year, one-year old, and two-year old) plateaued at 40% in 2014 (Figure 4) and 50% in 2015 (Figure 5).

For one-year old and two-year old foliage at relatively high larval densities, as in 2015, relationships between spruce budworm density and defoliation were parabolic (one-year old $\Delta AIC = 22.7687, 5.9561$; two-year old $\Delta AIC =895.06$; Table 6 AIC). For these foliage classes, defoliation began to decline for densities over four larvae per current year shoot (Figure 5). In 2014, no cages had budworm densities higher than 2.5 larvae per shoot so we were unable to test for similar declines.

DISCUSSION

Interspecific competition is routinely cited as playing a critical role in determining insect assemblages (i.e. patterns of distribution, abundance, and diversity) (Connell 1983; Schoener 1983; Jermy 1985; Denno et al. 1995; Begon et al 2005). Janzen (1973) considered all insects sharing a common host to be in competition with one another, regardless of niche overlap or ecological similarity. Among insect-plant systems, conifers have been of particular interest because of their economic importance. Exploited conifers are often attacked by wood-boring beetles and by defoliators, either simultaneously or at different times in tree phenology. Several past studies have examined beetle attack-defoliator interactions on conifers. However, while we focused on the effects of phloem feeders on defoliators, most previous studies examined how defoliators affect beetles (eg. Annila et al. 1999, Wallin and Raffa 1999, Colgan and Erbilgin 2011). In several such studies, previous defoliation increased tree resistance to beetle attack, leading to higher beetle mortality (eg. Annila et al. 1999, Wallin and Raffa 1999, Colgan and Erbilgin 2011). Colgan and Erbilgin (2011) and Wallin and Raffa (1999), for instance, showed that defoliation by jack pine budworm negatively affected mountain pine beetle by inducing resistance of the tree through increased monoterpenes and fewer lesions after inoculation. Annila et al. (1999) found similar results on Scots pine after defoliation by common pine sawfly (*Diprion pini*) which led to negative impacts on the longhorn beetle

Monochamus carolinensis. Other systems show similar patterns between co-occurring herbivores, where the presence of a specific species affects the performance and survival of the other. For example, Moran and Whitham (1990) showed herbivory on *Chenopodium* sp. by a leaf-galling aphid led to an average of 54% host mass reduction. This in turn led to a reduction of a co-occurring root-feeding aphid by an average of 91%, and often eliminating the species entirely. The reason for asymmetry between responses to co-occurring herbivores is that many herbivores elicit physical, morphological, or chemical changes in their host. These changes can then render the host more resistant or less resistant to co-occurring herbivores, depending on the species (Kaplan et al. 2007).

Stressed trees, in general, have fewer resources that are allocated to growth and thus may produce fewer and/or smaller shoots (Waring 1987) – but our stressed treatment trees increased shoot production. Similar effects have been observed previously with conifer stands in Cape Breton, Nova Scotia, after spruce budworm defoliation (Piene 1996). Most studies of conifer responses to spruce budworm have focused on balsam fir and white spruce (Piene 1996), whereas responses of other, less susceptible conifers, such as red spruce, are poorly studied. At least for balsam fir and some spruce species, though, defoliation during peak outbreak can trigger release of dormant buds located on older twigs/branches (i.e. epicormic shoots), since trees are attempting to replace lost foliage (Stone 1953, Piene and Eveleigh 1996, Carroll and Quiring 2003). Such epicormic shoots could account for the increases in current-year shoot production in our stress treatments. In our study, stress treatments involving the severing of vascular tissues, either through girdling or beetle feeding, may explain why shoot production and shoot quantity were increased in stress treatments (except in 2015, where no effect on shoot length was observed). Unfortunately, we do not have data on shoot biomass, therefore it is uncertain if shoot allocation, measured as biomass, increased with shoot production.

Conifers respond to different degrees of stress in different ways. Conifer defensive mechanisms against wood boring beetles that destroy phloem and cambium tissues are either constitutive or induced to act against a current attack or future attacks. These defense mechanisms include resin accumulation in cells and channels in phloem, phytotoxins stored in phloem cells, mechanical properties in the wood (e.g., lignified cell layers) (Berryman et al. 1989; Franceschi et al. 2005), and locally occurring hypersensitive responses to attack (Berryman 1972, Bleiker and Uzunovic 2004). After multiple generations of attack by wood-boring beetles, the phloem can be destroyed completely around the bole of the tree. We simulated this effect artificially by mechanically girdling trees. Typically, a girdled tree is one in which the phloem is completely severed. Severing the phloem can be done by a narrow incision, or by the complete removal from the trunk of a wide cylinder of bark, with or without damage to the underlying tissue (Noel 1970). Girdled conifers remain alive in the short term (Noel 1970, Stone 1975, Wilson 2002) but the red spruce in our study were severely damaged and close to mortality by the next summer. While we use girdling as a way to simulate the results of multiple generations of wood beetle attack, the underlying mechanisms of the stresses clearly differ. While both stresses involve removing or severing of the phloem tissues, differences such as time scale (Flaherty et al. 2013), biotic factors that accompany wood boaring beetles (Franceschi et al. 2005), and tree defenses (Berryman et al. 1989; Franceschi et al. 2005) are extremely different between girdling and wood boring beetle attack. Since artifically girdling a tree with a chain saw is fast and aggressive, the tree has no time to respond and defend. This may force the tree to expend available and stored resources towards a last effort at survival or reproduction. In comparison since the phloem tissue is not severed completely when beetles start to attack, there is time to put resources into defensive mechanisms. This difference in the hypothetical re-allocation of resources done during girdling and beetle attack may cause a bias in our conclusions since we are interpreting girdling as a analogous to multiple generations of beetle attack. As a result, it would certainly be valuable to conduct experiments like ours with trees under many years of beetle attack. Unfortunately, such experiments will be logistically challenging.

The high larval mortality that resulted in our experiment, 77 % in 2014 and 90% in 2015, was accounted for during analysis by using densities that were originally placed on branches at the start of the season. Since mortality could have happened at any point throughout the season, analyzing data with survivorship from the end of season would likely overestimate the per capita effect of larvae. There are consequences of analyzing data with either start or end of season densities, but since larvae may inflict damage on the host before they die, using end-season densities would significantly under-estimate the densities responsible for observed damage.

Larval mortality during our experiment was high compared to natural larvae. Morris and Miller (1954) show 26.5% fourth-instar mortality and 38.6% second-instar mortality, compared to 77% fourth-instar and 90% second-instar observed in our experiments. This could be due to rearing larvae on artificial diet in laboratory conditions prior to using them in the field.

Density-defoliation relationships are available for select tree species (West and Carter 1992, Régnière and Cooke 1998) but cannot be extrapolated to red spruce due to the differences in inherent growth rates and foliage biomass per shoot (Hennigar et al. 2008). For example, Régnière and Cooke (1998), found that it took 0.7 budworm larvae per bud to completely defoliate a balsam fir tree, which is approximately 27.6 per 45cm branch. Another estimate for balsam fir density-defoliation relationships by West and Carter (1992) found that at 0.5 larvae per bud, 62% of the shoot would be defoliated. In our experiments on red spruce, defoliation generally rose with budworm density, although it plateaued over larval densities of around 0.5 per current-year shoot and declined when densities exceeded 4 in 2015. However, at high densities, we see a complex relationship when larvae are forced to backfeed. We only see these high densities in 2015, since densities used in 2015 were elevated from the previous year to account for higher larval mortality when younger, smaller larvae are used (Lawrence et al 1997, MacLean and MacKinnon 1997).

While our experiment was designed to reveal effects of phloem feeding beetle attack on spruce budworm relationships, our most interesting finding may be the shape of the density-defoliation relationships at high budworm densities. While the range of densities we used provides less resolution for low densities typical of the beginning of outbreaks, they allow us to observe what happens at the extremely high populations, such as at the peak of outbreaks, when competition for food is intense. For comparison, Ostaff and MacLean (1989) recorded maximum densities equivalent to 318 third-instar larvae per branch (pers. comm. D. MacLean, University of New Brunswick; Appendix 1) in Cape Breton, Nova Scotia, in 1980 during peak outbreak. High densities such as these, have commonly been anecdotally reported before, and are expected to lead to high larval mortality. Since branches were exposed to excessively high population densities, larval spruce budworm may starve, due to high competition for food and lack of availability.

Most density-defoliation relationships focus on population densities below those necessary to achieve 100% defoliation (e.g. Johns et al. 2006; Parsons et al. 2005), and few studies have observed what happens when densities exceed that threshold. Our study suggests that there may be some insight to be derived from testing relationships at much higher densities. In 2015 particularly, defoliation of current-year foliage increased linearly with larval density up to about 0.5 larvae per current-year shoot, and then plateaued – as one might predict when the resource become overexploited. However, when we look at older foliage (e.g, one-year old and two-year old) the relationship was actually parabolic, with defoliation peaking at approximately 4 larvae per shoot and then declining for greater densities. We analyzed different models to examine which one better fit our data, using delta AIC values. In 2015, a non-linear saturated model was significantly better than a linear model, and the non-linear, parabolic, model was a significantly better fit than both (both delta AIC values were greater than 2). We suspect that this parabolic relationship for older age-classes reflects the extreme pressure excessively high densities of early-instar larvae put on the availability of the preferred current-year foliage. Exhaustion of current-year foliage forces young larvae to back-feed, and older foliage is tougher and more difficult for larvae to consume (Pureswaran et al. 2016) – especially early-instar larvae. The result is likely to be high mortality – even of larvae that could have successfully back-fed, had they had access to enough current-year foliage to grow large enough for backfeeding. Our data suggest that extremely high population densities may lead to higher mortality of early instar larvae, compared to merely high densities. Spruce budworm populations can collapse rapidly at the end of an outbreak and there is evidence that early-instar mortality associated with foliage depletion can contribute to this collapse in conjunction with death from natural enemies (Royama 1984, Régnière and Nealis 2008).

From an applied standpoint, the peaking of defoliation at high densities, and dropping at extremely high densities is interesting. Budworm outbreaks have been controlled using a 'foliage protection' strategy for the past half century, which entails stand-by-stand management focusing on treating high value stands, where defoliation is threatening significant growth yield loss or mortality. Other surrounding forests, or forests that are soon to be harvested, are left unprotected for the outbreak to run its course. Total defoliation is the important factor for the survival of the host tree. Spraying could decrease present larval densities, but not actually decrease total defoliation. During these outbreaks, controlling populations in the high value stands by spraying insecticide will potentially only be beneficial if high-density populations are reduced to very low levels. If densities are reduced to from extremely high levels to merely high population levels, spruce budworm may do more damage than management intended: current-year foliage defoliation will not change, but backfeeding may increase in a specific stand, leading to larger healthier larvae and increase population level recruitment. Other possibilities may be if these high-value stands have high densities, then to spray these areas to reduce to very low population levels, and leave the extremely high-density cores untreated to collapse themselves due to starvation.

In Nova Scotia, this complex spruce budworm backfeeding phenomena that we observed on red spruce may be important to the management and conservation of that species. When spruce budworm second-instar larvae emerge in the spring from hibernacula, they begin feeding on current-year growth of their host species. Red spruce bud burst in Nova Scotia is approximately 2 weeks after spruce budworm emergence; therefore, larvae are forced to mine current-year buds. During our experiment, this mining of buds was observed in both years when larvae were put on branches before complete bud burst. Mining buds significantly decreases the amount of nutritious current-year foliage spruce budworm larvae consume, and forces larvae to backfeed on older foliage. From a management or conservation perspective for red spruce, depending on the population densities, backfeeding could potentially be worse for the trees.

Our prediction that effects of simulated and natural BSLB attack would increase density-defoliation relationships was not borne out. Instead while both simulated and natural BSLB attack did impact the growth of red spruce, they did not change the density-defoliation relationships of spruce budworm. Our most interesting finding did not actually have to do with the effects of BSLB, but in the trend in defoliation with budworm density. In particular, we saw less defoliation at extremely high larval densities than at high densities. This suggests the possibility of stress affecting performance of budworm larvae, and in turn, of longer-term feedbacks via budworm densities in future generations. We test this hypothesis in Chapter 3.

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Table 1. Summary of 2014 and 2015 Sandy Lake, Hammonds Plains, site characteristics

Year	DBH (cm; avg ±SE)	GPS	Age of SBW larvae when placed on tree	Stress Treatments
2014	20 ± 4.8	N 44° 44’8.236” W 63°40’1.88”	4th Instar	1. Control 2. Girdling 3. Girdling + beetle attack
2015	19.2 ± 4.7	N 44°44’6.227” W 63°40’1.567”	2nd Instar	1. Control 2. Girdling 3. Girdling +beetle attack 4. Beetle attack

Table 2: Impact of wood-boring beetle and girdling on growth and development of *Picea rubens* in 2014 and 2015.

A) Number of current-year shoots

Year	Factor	df	MS	F	*P*
2014	Treatment	2	9882	5.47	0.0054*
	Residuals	110	1807		
2015	Treatment	3	4828	2.59	0.059
	Residuals	74	1861		

B) Tukey's Post Hoc test for number of current-year shoots in 2014

Year	Treatments	diff	lwr	upr	*P* adj
2014	Control x Girdled	25.99	2.70	49.30	0.025*
	Control x Girdled + Beetle attack	28.48	5.71	51.25	0.01*
	Girdled x Girdled + Beetle attack	2.49	-21.51	26.48	0.97

C) Terminal length of current-year shoot

Year	Factor	df	MS	F	*P*
2014	Treatment	2	37.01	7.28	0.00107*
	Residuals	110	5.08		
2015	Treatment	3	2.11	0.47	0.701
	Residuals	74	4.45		

D) Tukey's Post Hoc test for Terminal length of current-year shoots in 2014

Year	Treatments	diff	lwr	upr	*P* adj
2014	Control x Girdled	1.79	0.56	3.03	0.002*
	Control x Girdled + Beetle attack	1.54	0.33	2.75	0.008*
	Girdled x Girdled + Beetle attack	0.26	-1.02	1.53	0.88

Table 3: Summary of ANCOVA analyses evaluating impact of wood-boring beetle attack and girdling on spruce budworm density – defoliation relationships established in field experiments in 2014.

Year	Factor	df	MS	F	*P*
2014	Girdled	1	0.003	0.061	0.805
	Density	1	9.637	215.358	$<2e^{-16}$*
	Girdled x Density	1	0.008	0.184	0.668
	Residuals	283	0.045		

Table 4: Summary of ANCOVA analyses evaluating impact of wood-boring beetle attack and girdling on spruce budworm density – defoliation relationships established in field experiments in 2015.

Year	Factor	df	MS	F	*P*
2015	Girdled	1	0.041	0.456	0.5
	Beetle attack	1	0.144	1.606	0.206
	Density	1	7.149	79.778	$<2e^{-16}$*
	Girdled x Beetle attack	1	0.002	0.023	0.881
	Girdled x Density	1	1.189	13.267	0.0003*
	Beetle attack x Density	1	0.432	4.817	0.292
	Girdled x Beetle Attack x Density	1	0.121	1.348	0.246
	Residual	236	581		

Table 5: Akaike information criterion (AIC) values used to estimate the quality of each regression relative to each other, for the impact of wood-boring beetle attack on *C. fumiferana* density-defoliation relationships from 2014. Bold values are best fits, using the delta AIC. If delta AIC is larger than 2, evidence for the relationship with smaller value is better quality.

	Treatment	Linear model	Non-Linear model (Saturated)	Delta AIC
Total Defoliation	Control	789.20	**781.28**	7.92*
	Girdled	1593.30	**1509.09**	84.21*
Current year defoliation	Control	954.31	**884.41**	69.91*
	Girdled	1877.29	**1663.82**	213.47*
One-year old defoliation	Control	**820.29**	821.80	1.51
	Girdled	1682.44	**1659.94**	22.50*
Two-year old defoliation	Control	**812.06**	832.48	20.42*
	Girdled	1662.68	**1562.35**	100.33

*****Delta AIC > 2 evidence that smaller value is a better fit for data

Table 6: Akaike information criterion (AIC) values used to estimate the quality of each regression relative to each other, for the impact of wood-boring beetle attack on *C. fumiferana* density-defoliation relationships from 2015. Bold values are best fits, using the delta AIC. If delta AIC is larger than 2, evidence for the relationship with smaller value is better quality.

	Treatment	Linear model	Non-Linear model (Saturated)	Non-Linear	Delta AIC
Total Defoliation	Control	427.86	**398.40**		29.46*
	Girdled	910.47	**840.98**		69.50*
	BSLB	1371.33	**1276.58**		94.75*
Current year defoliation	Control	476.81	**391.87**		84.93*
	Girdled	1014.03	**852.46**		161.57*
	BSLB	1488.43	**1330.54**		157.89*
One-year old defoliation	Control	452.56	435.75	**429.7900**	22.77* 5.96*
	Girdled	927.79	**864.76**	893.4277	63.03* 28.67*
	BSLB	1428.83	**1388.23**	1407.876	40.61* 19.64*
Two –year old defoliation	Control	416.66	**409.01**	410.70	1.69
	Girdled	895.82	**872.51**	879.16	6.65*
	BSLB	905.39	895.933	**895.06**	0.87

Figure 1– Photos from Sandy Lake, Hammonds Plains, of treatment trees in 2014. a) Girdled with chain saw b) girdled with chain saw and exclusion cage on trunk

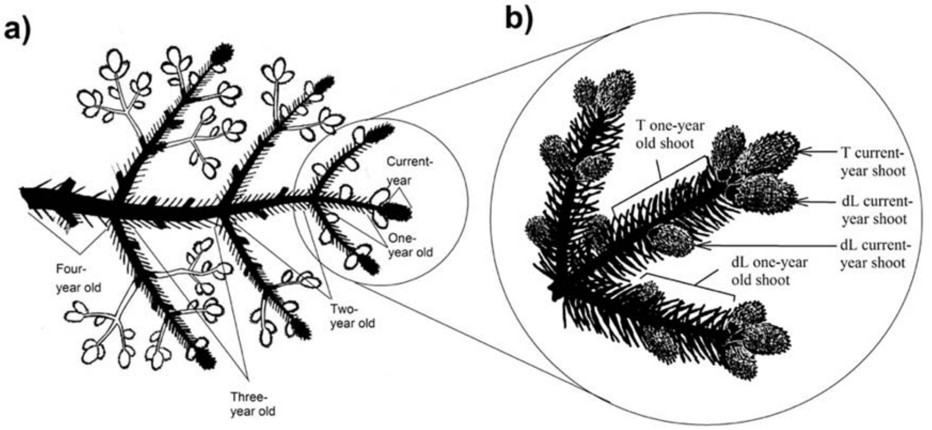

Figure 2 – a) Schematic representation of a red spruce branch where defoliation was visually estimated for all age-classes shown (current-year, one-year old, two-year old, three-year old and four-year old). b) Schematic representation of the tip of a red spruce branch, including current-year growth and one-year old growth. Terminal (T) and distal lateral (dL) current-year and one-year old shoots were measured for growth estimates, using number of current year shoots and lengths of T and dL branches.

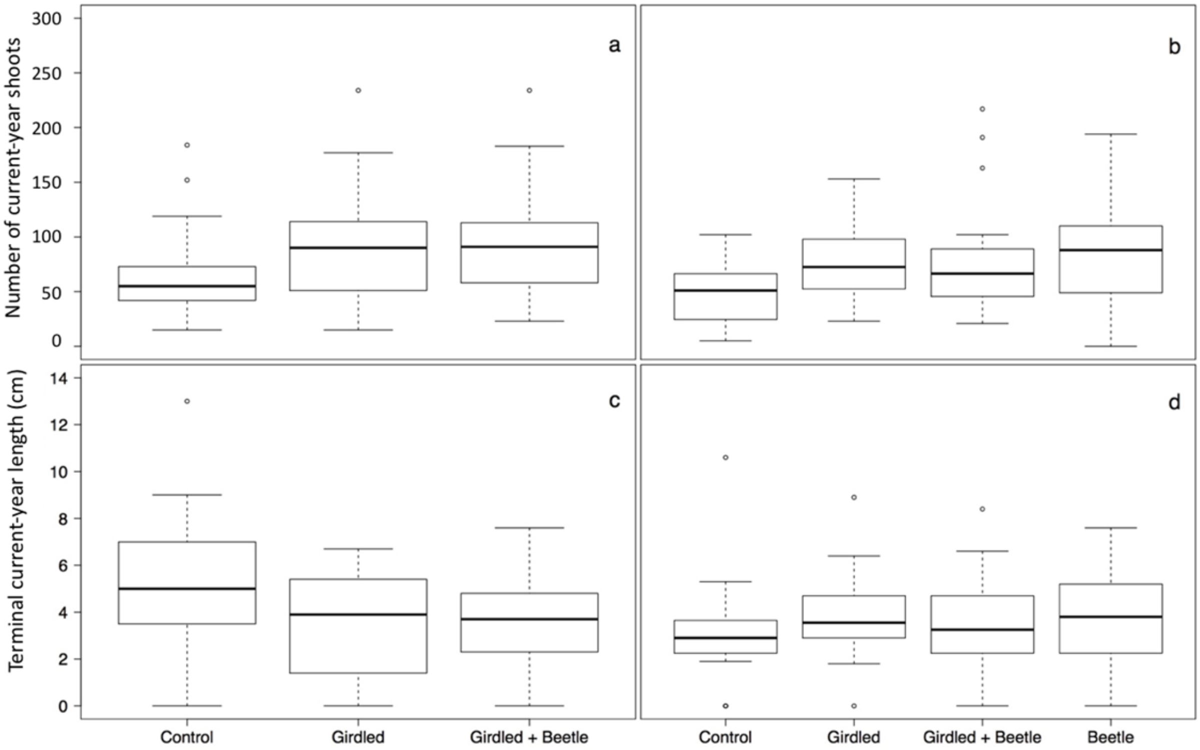

Figure 3 – Impact of wood-boring beetle attack and girdling on *Picea rubens* growth and development, using terminal current year shoot length and number of current year shoots as proxies from 2014 (a, c) and 2015 (b, d). Center line is median; box shows 25th/75th; whiskers show 10th/90th percentiles; and dots show 5th/95th.

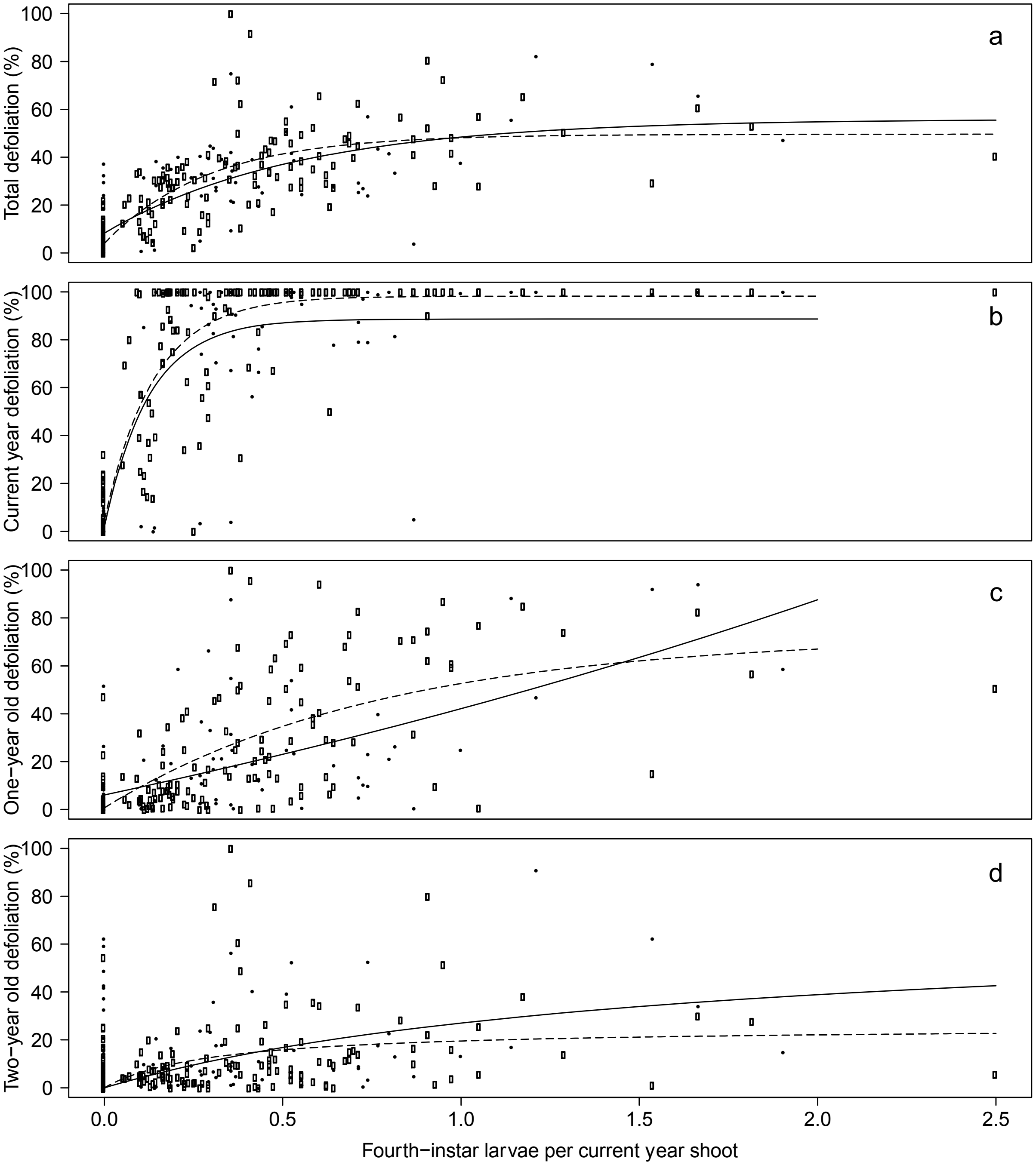

Figure 4: Impact of wood-boring beetle attack and girdling on relationships, from 2014, between the number of fourth instar *C. fumiferana* larvae per current year shoot in sleeve-cages on 45 cm branch and mean percent (a) total defoliation (average of current-year, one-year old, and two-year old), (b) current year shoots, (c) one-year old shoots, and (d) two-year old shoots. The data of each treatment are represented by different shades (control = black, girdled = gray), while regressions of each treatment are represented by different lines (solid = control, dashes = girdled).

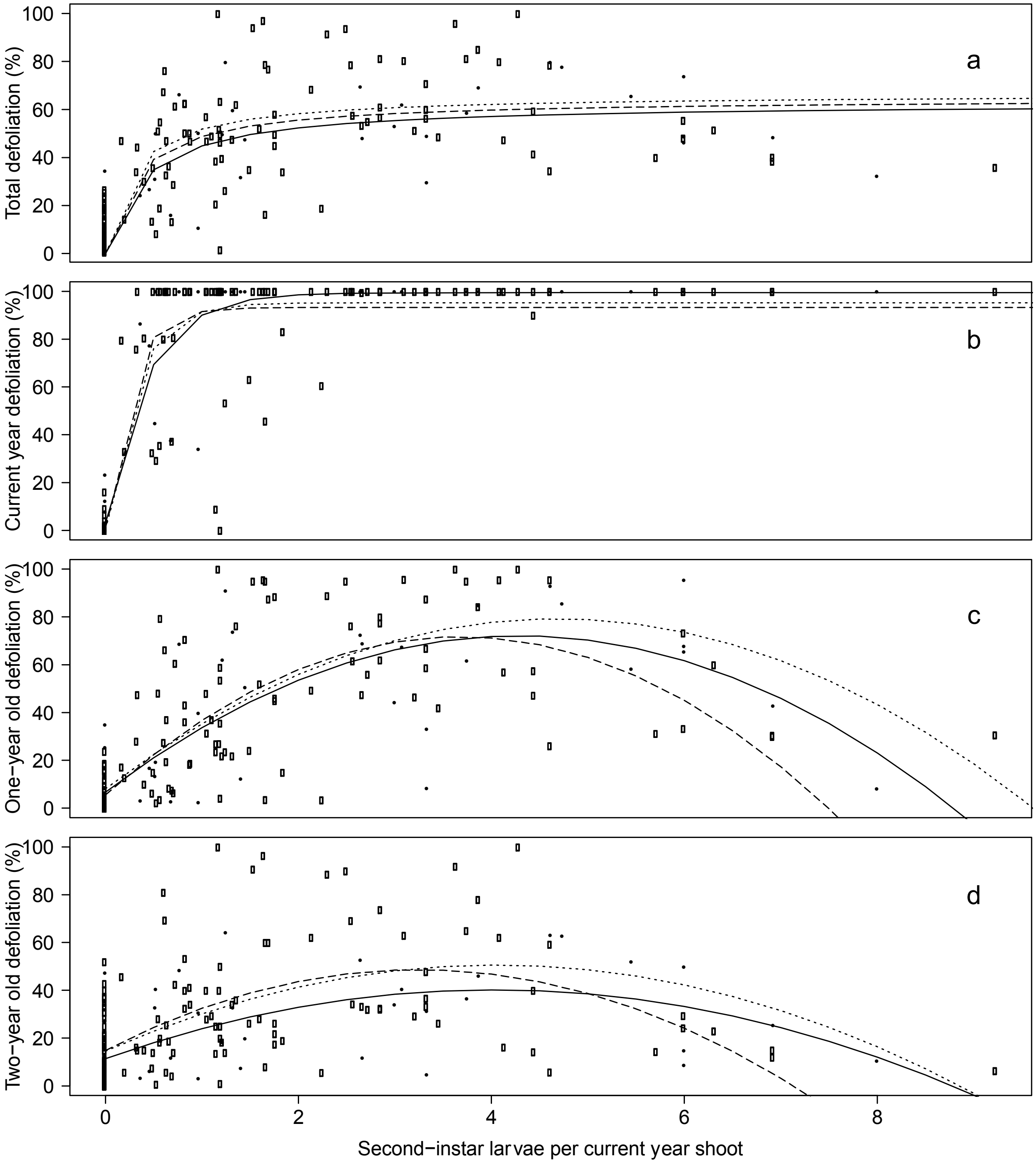

Figure 5: Impact of wood-boring beetle attack and girdling on relationships, form 2015, between the number of second instar *C. fumiferana* larvae per current year shoot in sleeve-cages on 45 cm branch and mean percent (a) total defoliation (average of current-year, one-year old, and two-year old), (b) current year shoots, (c) one-year old shoots, and (d) two-year old shoots. The data of each treatment are represented by different shades (control = black, girdled = gray), while regressions of each treatment are represented by different lines (solid = control, dashes = girdled).

CHAPTER 3: THE EFFECT OF WOOD-BORING BEETLE ATTACK AND GIRDLING ON SPRUCE BUDWORM LARVAL PERFORMANCE ON RED SPRUCE

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ABSTRACT

Spatially separated herbivores that exploit a shared host may interact indirectly when they alter the quality or quantity of available host tissues. Aside from their collective impact on their host's health, herbivores attacking different tissues of the same host may also reduce or enhance the performance of one another. A potential example of this interaction is the outbreaking spruce budworm (*Choristoneura fumiferana* Clem.) and exotic brown spruce longhorn beetle (*Tetropium fuscum* Kirby). Both are important forest pests in Eastern Canada, and have the potential to spatially and temporally overlap in range. We describe research assessing the indirect interaction between brown spruce longhorn beetle and spruce budworm, and the consequences of this interaction for spruce budworm performance. We conducted field experiments, in which red spruce trees were infested with herbivores in a 2 x 2 factorial design (both, one, or neither species), and

performance of spruce budworm adults was assessed using body size (a correlate of fecundity) and survival. In both seasons, there was a negative effect of budworm density on budworm survival, but no effect of beetle attack on budworm survival. In 2014, there were effects of budworm density and beetle attack on forewing length of spruce budworm adults, but not in 2015. Since spruce budworm adult fecundity and survival were reduced by simulated and natural beetle attack, and by high intraspecific competition; the pending overlap of these two species invasion ranges could potentially influence the distribution and survival of outbreaking spruce budworm in areas where brown spruce longhorn beetle occurs.

INTRODUCTION

Spatially separated herbivores that exploit a shared host may interact indirectly when they alter the quality or quantity of available host tissues. Aside from their collective impact on their host’s health, herbivores attacking different tissues of the same host may also reduce or enhance the performance of one another (Morris et al. 2007). Such indirect competition has been more frequently observed in systems where there is an exotic or introduced species rather than in a system where all the potentially affected herbivores are native (Denno et al. 1995). Heard and Kitts (2012) have suggested that the escalated impact may be because invasive species have evolutionarily novel associations and therefore more severe potential impact on native hosts; if so, then more severe impacts on other herbivores will probably follow.

A potential example of such indirect interaction is that between the outbreaking spruce budworm and exotic brown spruce longhorn beetle. Spruce budworm (*Choristoneura fumiferana* Clem.) is an important forest pest in northeastern North America. Spruce budworm is a significant defoliator of balsam fir (*Abies balsamea* (L.) Mill.) and spruce trees (*Picea* spp.). Previously, spruce budworm has reached outbreak densities in New Brunswick, and between 1965 -1992, budworm defoliation affected over 90% (6.8 million hectares) of the province’s forest (Zhao et al. 2014). The current outbreak, which started in Quebec, has affected 7 million hectares in Quebec alone (NRCAN, Healthy Forest Partnership). This outbreak of spruce budworm in northern New Brunswick coincides with an invasion of brown spruce longhorn beetle (*Tetropium fuscum* Kirby, BSLB) in Nova Scotia. BSLB is a phloem feeding beetle currently attacking spruce trees in Nova Scotia. Adults lay eggs on the bole of the tree, under bark scales and in crevices, then once larvae hatch, they feed on phloem tissues and after multiple generations can kill the host tree. The impacts of the indirect interaction between spruce budworm and BSLB are still unknown, since BSLB established after the previous spruce budworm outbreak in Nova Scotia. This outbreak reached its peak during the 1970s, and lasted until late 1980s. As a result, little is known of how BSLB might indirectly interact with budworm and whether BSLB could influence budworm performance and thus outbreak dynamics.

Here, we report field studies seeking to understand how attack on red spruce by BSLB might impact spruce budworm performance. Determining average fecundity in spruce budworm populations is essential when evaluating spruce budworm population dynamics. We estimated fecundity using a proxy, wing length. Numerous studies show wing length to be correlated with fecundity in insects (e.g., Packer and Corbet 1989; Bellinger et al. 1990; Lounibos et al. 1990; Livdahl and Wiley 1991). We compared the performance of spruce budworm on healthy red spruce trees to those placed on trees that had been stressed either by forcing BSLB to lay eggs on trees (i.e., to create galleries) or by girdling trees to simulate high levels of beetle attack. Budworm were placed on branches of each study tree at a range of different population densities to simulate different potential population levels. We used these experiments to measure the indirect impact of BSLB attack and a simulation of long-term BSLB attack on spruce budworm performance (measuring survival and wing length, with the latter a proxy for fecundity).

METHODS

For in-depth description of the study species' life history and selected site characteristics, see Chapter 2 (pg 13).

Sleeve cage experiment setup

In 2014, we chose 60 trees haphazardly chosen, along with 40 trees in 2015 at Sandy Lake, near Halifax, Nova Scotia, before budburst in the spring. We divided trees into separate stress treatments involving natural and simulated wood-boring beetle attack. The first treatment was a control, where there was no beetle attack on the trees. Treatment #2 was where we girdled all trees to simulate multiple generations of beetle attack. For treatment #3, we girdled the trees, and added mating pairs of beetle in exclusion cages to the trunk. In 2015, we added a fourth treatment, in which we just had mating pairs of beetles in exclusion cages on the trunk of our trees, without girdling.

Within each tree, we selected five branches, and then placed spruce budworm larvae on the branches in sleeve cages in different densities. We used spruce budworm larvae from a lab reared colony from the Atlantic Forestry Center in Sault Saint Marie, Ontario, Canada. In 2014, we reared spruce budworm larvae under laboratory conditions until they reached fourth instar, and then placed on branches after bud burst from 10 to 12 of June in densities of 0, 10, 20, and 40 per branch. In 2015, second-instar larvae were placed directly on branches prior to any feeding, from the 20 to 25 of May, prior to budburst in densities of 0, 30, 90, ad 120. For further detail, see Chapter 2 (Methods, pg.13).

At the end of the season (early July), we collected spruce budworm adults from branches and preserved them at -18°C.

Forewing measurements

Spruce budworm moth forewings were removed to measure using a dissecting microscope. Forewings lengths were then measured to the nearest 0.1 mm (Figure 6).

Statistical analysis

We used R version 3.1.3 to complete the statistical analysis of the impact of wood-boring beetle on spruce budworm performance.

We used one-way ANCOVA to compare the average wing lengths per branch between treatments and survival between treatments for each of the two years. Tukey's honest significant test was used to compare average wing-lengths between treatments in 2014.

In 2014, the experimental design was a split plot, and we used a mixed-factor analysis of co-variance to test for differences between treatments by looking at the differences in slopes, intercepts, and their interactions. There are three levels of treatment, one factor with three levels of stress treatment (control, girdling, and girdling plus BSLB). We used Student-Newman-Keuls tests to determine which treatments differed in wing-length and survival. We used a logit transformation to transform our data.

In 2015, a fourth stress treatment was added, changing the design to a two by two factorial (girdling × BSLB). The analysis is otherwise unchanged from 2014.

RESULTS

Overall spruce budworm survival through to pupation in our experiments was 23% in 2014 and 10% in 2015.

Overall, there was a negative effect of density on forewing length in 2014 (Figure 7a), where forewing length decreased by 0.25 mm, 0.5 mm, and 0.25 mm per spruce budworm per current-year shoot for control, girdled, and girdled plus BSLB treatments ($P < 0.05$, Table 7). There was no effect of density on survival in 2015 (Figure 7b), and $P = 0.072$ (Table 8).

In 2014, density had a negative effect of on survival (Figure 8a), where survival decreased by 0.05, 0.3, and 0.1 per spruce budworm per current-year shoot for control, girdled, and girdled plus BSLB treatments respectively, $P < 0.05$ (Table 9). In 2015, density had a negative effect of on survival (Figure 8b), where survival decreased by 0.05, 0.05, 0.05, and 0.1 per spruce budworm per current-year shoot for control, girdled, girdled plus BSLB, and BSLB treatments respectively, $P = 0.012$ (Table 10).

Once density was controlled for by covariate, we were able to examine the effect of treatment. There was no effect of treatment on survival in 2014 ($P = 0.083$) or in 2015 (Girdling treatment: $P = 0.74$, BSLB treatment: $P = 0.12$). Forewings were on average 0.5 mm shorter in 2014 on stressed treatment vs. control trees (Figure 7a) with a $P < 0.05$ (Table 7). In 2014 forewing lengths differed between control trees and girdled/girdled plus beetle attack trees, but not between girdled and girdled plus beetle attack trees (Table 7)

There was no effect of treatments on the average wing length in 2015 (Figure 7b) (girdled $P = 0.09$, BSLB $P = 0.06$). There was, however, an interaction between BSLB treatment and larvae densities per shoot (Table 8), but the interaction was subtle (P = 0.04). A second ANCOVA was analysed without the interactions of BSLB, girdling, and densities to remove variance and there was still no effect of treatments on forewing length.

DISCUSSION

Survival was low in both 2014 and 2015, with only 23% and 10% larvae surviving through to pupation respectively. Previous studies have shown similar survivorship, eg. Reichenbach and Stairs (1984) showed survival as low as 20% when spruce budworm were exposed to stress (temperature and humidity) on trees. Other studies show low survival of spruce budworm on red spruce, Mattson et al. (1991) found 23% survival of spruce budworm when exposed to red spruce as a host. Both Blais (1957) and Mattson et al. (1991) conclude that black and red spruce are inferior as hosts for spruce budworm, largely due to their late phenology of budburst and shoot elongation, relative to fir and white spruce. This delay in phenology creates asynchrony between spruce budworm larvae and host, leading to lack of available early spring feeding sites (Shepherd 1985; Volney 1985).

In 2014 and 2015 survival was reduced at high densities of spruce budworm larvae. At higher density, the lower survival rates are presumably due to intraspecific competition. At low population levels, budworm larvae prefer feeding on current-year growth of the host tree (Blais 1952 1953; Mattson et al. 1983). At high population levels, which are expected during severe infestations at the peak of outbreaks, larvae are forced to feed on old foliage, or starve. Older foliage (>1-year old) is nutritionally inferior to the current-year needles (Blais 1952, 1953; Mattson et al. 1991; Bauce et al. 1994). As a result, survival of these smaller larvae and fecundity of surviving adults are substantially reduced (Blais 1958; Miller 1963; Mott 1963; Chapter 2). Blais, in both laboratory (1953) and field studies (1952), also found a decrease in the fecundity of spruce budworm adults issuing from a population that was forced to feed on old foliage.

Our study demonstrates that there is an influence of girdling on the performance of spruce budworm adults. Girdling was used as a stress in both years to simulate multiple generations of beetle attack (Chapter 2). These relationships show an overall negative effect of beetle attack on fecundity in 2014, with fewer females and smaller females on stressed trees; in 2015, moths were not significantly smaller, but fewer survived. A potential explanation for the difference in results between years could be that the initial larval instars placed on branches and duration of development differed between experiments in 2014 and 2015. 2014 larvae were reared on artificial diet, where as 2015 larvae were not. This may also account for the difference in the sizes between the two years, since 2015 solely fed on foliage.

When plants are under stress, the stress on the plant has been considered both beneficial and detrimental to the insect herbivores. There is evidence that some herbivores prefer more vigorous plants or plant modules. Price (1991) proposes that plants or plant modules which are growing vigorously, or have grown vigorously, to become relatively large in a population of plants or modules, are favorable to certain species of herbivores. But stressed plants are often argued to be better hosts for insect herbivores, perhaps because of increases in soluble nitrogen available in the tissues consumed or because abiotic and biotic stresses are shown to increase the suitability of some hosts for insects (White 1984). BSLB prefer stressed trees in its native range, as do other beetles attacking trees, such as spruce beetle, *Dendroctonus rufipennis* (Juutinen 1955; Furniss and Carolin 1977). Rouault et al. (2006) also showed that defoliators profited from a drought that stressed trees in 2003 in Western Europe. This evidence is thought of not as an alternative to how plants are thought to react to stress by Price (1991), but at the opposite end of the plant and herbivore interaction spectrum. Our system is similar to how stress hurts the insect herbivore, since physical damage to the host tree did have a negative impact on fecundity of spruce budworm adults (fewer and smaller females), this interaction does not comply with the stress is beneficial category of how stress on hosts affects herbivores. Instead, the stress of beetle attack on red spruce hinders or hurts the performance of adults, though our results suggest that these effects may be mild.

In 2014, we saw a significant reduction in the size of the adult budworm on stressed trees. The bodies of our adult specimens were in poor condition, since branches were harvested at the end of the season, when budworm adults were dead; therefore, we were unable to sex the adults. Although unbiased estimates of sex ratios for local populations are difficult to obtain due to gender-specific behavioral differences influence the catchability. Sex ratios from multiple different sampling procedures were not markedly different from 1:1 (Miller 1963; Rhainds and Heard 2014), therefore we can assume that approximately half our surviving population are females, and can infer fecundity for them. It has previously been shown that the potential fecundity of females from spruce trees increased by an average of 69 eggs for each 1 mm increase in fore wing length (Thomas et al. 1980). With the decrease in potential fecundity from the trees with beetle attack, we could expect a significantly smaller amount of potential eggs to be laid.

Population growth of spruce budworm relates to the product of survival and fecundity. Since beetle attack had significantly reduced fecundity of spruce budworm adults and high intra-specific competition reduced survival of adults, it would seem that the pending collision of these two population ranges would reduce populations of budworm when at peak densities. How these two effects might interact may merit further study. If beetle attack reduces fecundity enough to moderate competition among larvae in future years, then the reduction in budworm population size might be less than expected by a simple additive prediction. Longer-term experiments would be needed to shed light on this prediction, but of course such experiments will be logistically difficult. Efforts to predict and manage spruce budworm outbreaks should consider interactions with other co-attacking herbivores.

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Table 7: Summary of average wing length of spruce budworm and larvae per branch in 2014

Year	Factor	df	MS	F	*P*
2014	Girdled	1	7.94	16.74	7.03e-05*
	Density	1	13.774	29.06	2.73e-07*
	Girdled x Density	1	0.023	0.049	0.825
	Residuals	147	0.474		

Tukey's Post Hoc test for average wing length in 2014

Year	Treatments	diff	lwr	upr	*P* adj
2014	Control x Girdled	0.604	0.259	0.948	0.00016*
	Control x Girdled + Beetle attack	0.374	0.025	0.723	0.0324*
	Girdled x Girdled + Beetle attack	0.229	-0.108	0.567	0.2435

Table 8: Summary of average wing length of spruce budworm and larvae per branch in 2015

Year	Factor	df	MS	F	*P*
2015	Girdled	1	0.826	2.918	0.093
	BSLB	1	1.016	3.589	0.063
	Density	1	0.951	3.360	0.072
	Girdled x BSLB	1	0.709	2.506	0.119
	Girdled x Density	1	0.482	1.705	0.197
	BSLB x Density	1	1.221	4.315	0.043*
	Girdled x BSLB x Density	1	0.418	1.476	0.230
	Residuals	55	0.283		

Table 9: Average survival of spruce budworm and larvae per branch in 2014 (logit transformation)

Year	Factor	df	MS	F	*P*
2014	Girdled	1	7.19	3.023	0.0832
	Density	1	192.21	80.847	<2e-16*
	Girdled x Density	1	1.47	0.619	0.4320
	Residuals	281	2.83		

Table 10: Average survival of spruce budworm and larvae per branch in 2015 (logit transformation)

Year	Factor	df	MS	F	*P*
2015	Girdled	1	0.153	0.111	0.739
	BSLB	1	3.394	2.470	0.118
	Density	1	8.834	6.430	0.012*
	Girdled x BSLB	1	0.024	0.018	0.894
	Girdled x Density	1	1.772	1.290	0.258
	BSLB x Density	1	4.345	3.163	0.077
	Girdled x BSLB x Density	1	1.074	0.782	0.38
	Residuals	186	1.374		

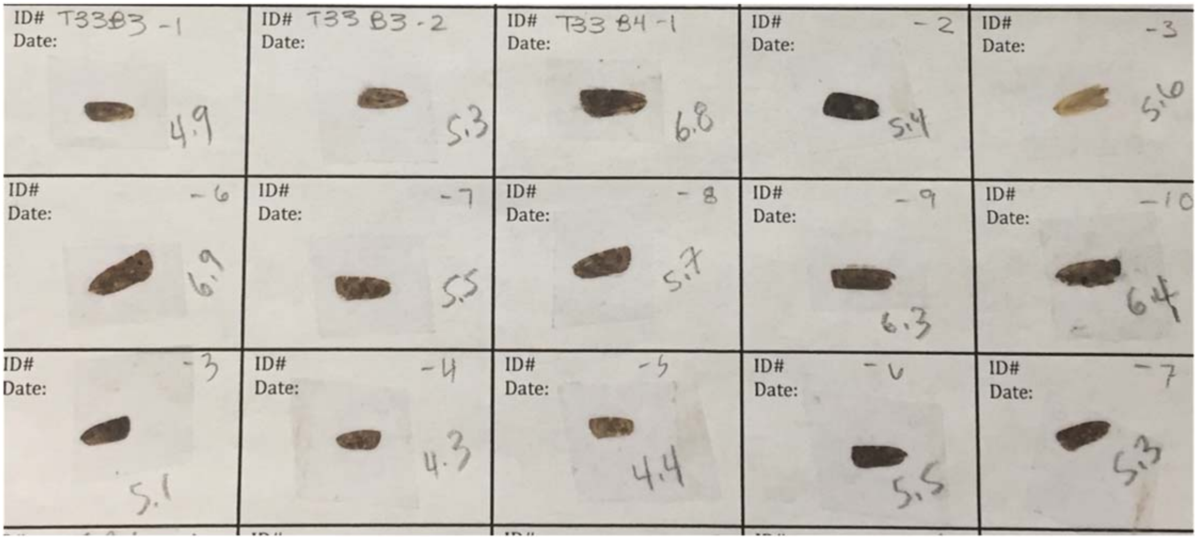

Figure 6: Forewings of adult *Choristoneura fumiferana* from 2014.

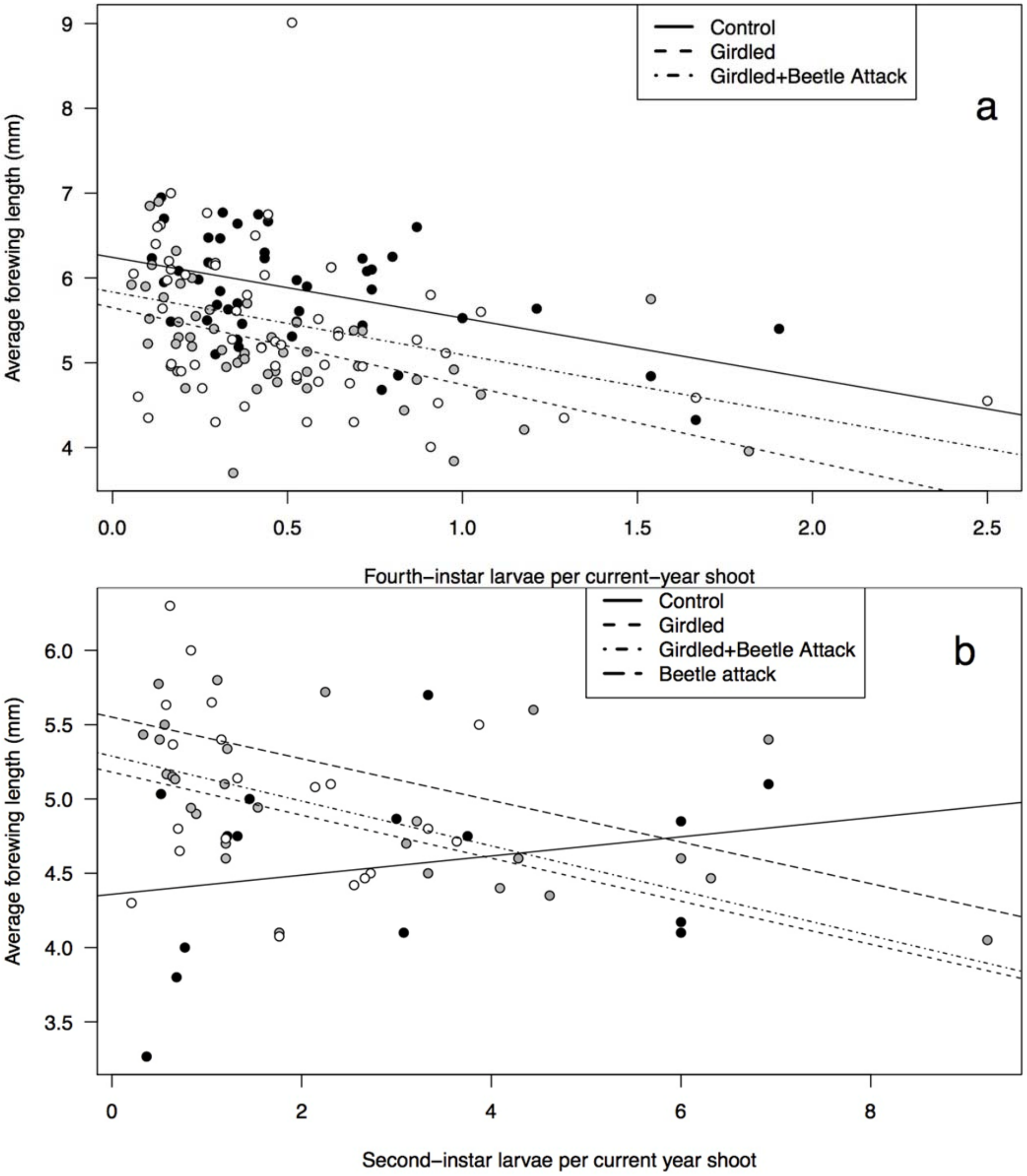

Figure 7: Impact of wood-boring beetle attack and girdling on relationships between the number fourth instar *C. fumiferana* larvae per current year shoot in sleeve-cages and average fore wing length (mm) per branch. Sleeve cages were placed over branches with manipulated, pre-selected, spruce budworm densities. (a) 2014 fourth-instar densities, the raw data of each treatment are represented by different shades (control = black, girdled = gray, girdled and beetle attack = white). (b) 2015 second-instar densities, the raw data of each treatment are represented by different shades (control = black, girdled = gray, girdled and beetle attack = white, beetle attack = dark gray).

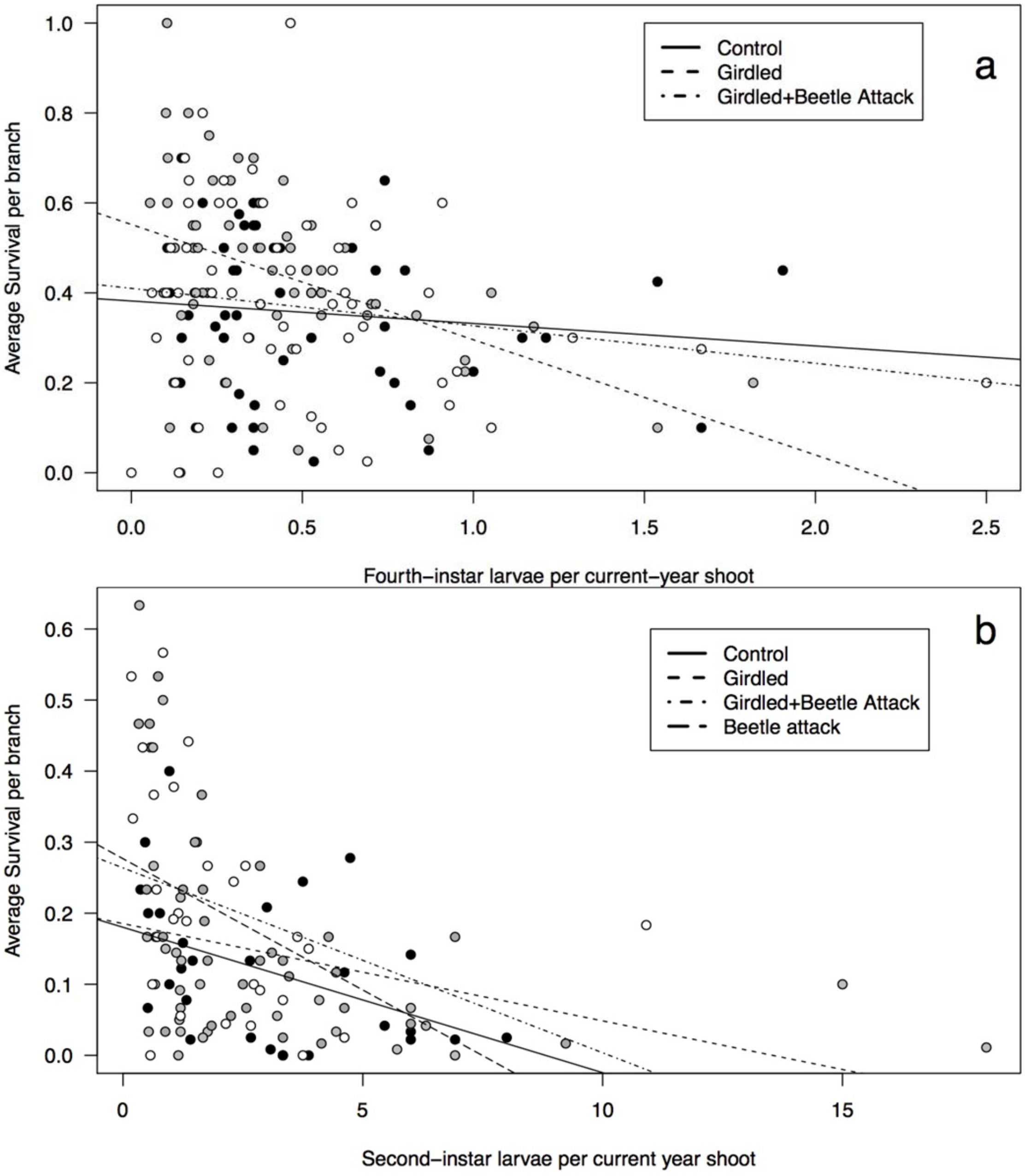

Figure 8: Impact of wood-boring beetle attack and girdling on relationships between the number second-instar *C. fumiferana* larvae per current year shoot in sleeve-cages and average fore wing length (mm) per branch. Sleeve cages were placed over branches with manipulated, pre-selected, spruce budworm densities. (a) 2014 fourth-instar densities. The raw data of each treatment are represented by different shades (control = black, girdled = gray, girdled and beetle attack = white). (b) 2015 second-instar densities. The raw data of each treatment are represented by different shades (control = black, girdled = gray, girdled and beetle attack = white, beetle attack = dark gray).

CHAPTER 4 – GENERAL CONCLUSION

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My overall goal was to investigate the effects of brown spruce longhorn beetle damage on interactions between spruce budworm and its host. I approached this question through field experiments that focused on two main objectives. The first was to determine the effects of beetle attack on relationships between spruce budworm density and associated defoliation. The second was to assess the effects of brown spruce longhorn beetle feeding (and tree stress) on spruce budworm performance.

There are two main ways to look at the potential spruce budworm outbreak/ brown spruce longhorn beetle invasion collision. The first scenario is that beetle attack on red spruce forests in Nova Scotia and New Brunswick will create areas where spruce budworm will excel and be able to defoliate and perform better by attacking already stressed trees. This may lead to hotspots of high spruce budworm population densities. This scenario is the hypothesis that we examined, and we found that beetle attack, at least in the short-term, did not significantly positively influence the performance of spruce budworm. Results from my thesis show that simulated beetle attack did in fact have an impact on red spruce trees. Shoot production was increased, but the shoots were shorter in length. Beetle attack also had an indirect impact on spruce budworm development. Forewing lengths were significantly smaller on attacked trees, and therefore fecundity was likely to be lower. Density-defoliation relationships were not significantly affected by beetle attack, but the high population densities of budworm larvae did have an impact, a non-linear one, on defoliation. This may reflect intraspecific competition, and we speculate that it may have interesting implications for spruce budworm control. The fact that defoliation of older foliage age-classes is parabolic suggests that total damage and therefore total foliage consumption by the budworm population peaks at high densities. This suggests in turn that such high densities could maximize population level budworm production. If this is true, then it could be beneficial in the treatment of local, extremely high-density populations to only spray the areas with high densities while leaving the extremely high-density cores untreated to collapse via starvation. Field experiments testing this idea are needed before making concrete decisions for the best management practices. This concept is of particular interest for the conservation and management of red spruce in Nova Scotia. Since the phenologies of red spruce bud burst and spruce budworm spring emergence are asynchronous, we could see mining of buds and subsequent complex backfeeding relationships.

An alternative way to examine the potential spruce budworm and brown spruce longhorn beetle range overlap could be to examine the indirect impact of spruce budworm attack (on red spruce) on performance of BSLB. Brown spruce longhorn beetles have a difficult time attacking healthy trees (Juuitnen 1955), unless in extremely large population densities. Resistance of healthy trees could be an important factor containing or slowing the spread of the invasion. Stress on red spruce caused by spruce budworm attack could increase BSLB performance and thus increase the rate at which its invasion spreads. We did not examine this side of the interaction, although it is potentially important for the future health of spruce forests in Atlantic Canada. Future field experiments examining this relationship could be conducted once the next budworm outbreak has built within the range of BSLB. Defoliation levels, in this case, could be manipulated using foliage protection strategies, where pesticides or biological control methods treating specific forest areas are used to reduce defoliation. Conducting field experiments to examine this relationship before the range overlap of spruce budworm and BSLB presents some difficulties. Since BSLB is under quarantine in Nova Scotia (CFIA), it is not possible to relocate BSLB to stands where there are current high populations of spruce budworm. Therefore, experiments would have to be conducted in Nova Scotia, where budworm populations are dormant (NSDNR). Inflicting damage to host trees that is consistent with spruce budworm larval damage is difficult, but certain herbicides may be analogous.

One limitation of our research is that we were unable assess whether BSLB mating pairs actually reproduced viable offspring under the bark of the red spruce host. Therefore in 2014, when the girdling treatment seemed to overpower the BSLB mating pairs addition, we did not have the information to support BSLB also having an impact. In future studies examining the effects of BSLB or bark beetle attack, it would be beneficial to capture the emerging beetles the next season, or examine the bole for galleries inflicted by the specific beetle.

Effects of beetle attack on defoliators are plausible because damage to phloem disrupts flow, and hence availability, of photosynthates and other resources for both foliage and insects. Complete severing of phloem, or girdling, is not exactly equivalent to multiple generations of BSLB attack, as there could be other consequences of BSLB attack not shown in girdling (ex. foliage changes). It is challenging to inflict this level of damage with BSLB in a field experiment, as multiple year experiments pose logistical issues in the context of funding and academic schedules. Girdling has been used as an analogous substitute in other experiments looking at BSLB attack (Flaherty et al. 2011; Dearborn et al. 2016). Quantifying beetle attack on hosts would involve searching for emergence holes, galleries, or catching emerging beetles. This would be a worthwhile objective for future work. Overall, our study found no significant influence of beetle attack (or girdling, simulating longer-term and more intensive attack) on the percent of consumed foliage by budworm at any given density, although there were mild effects of both simulated (girdling) and more natural (beetle attack) stress on tree shoot growth and production.

The research we have conducted has contributed additional information to the potential range overlap of two forest pests in Atlantic Canada. Deciding on forest management practices and forest conservation practices is not possible without basic knowledge of potential implications of these interactions.

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APPENDIX 1

I converted larval counts reported per m^2 of foliage to counts per branch, for comparison with my present data. Ostaff and Maclean (1989) reported 1570 third-instar larvae per m^2. Using data supplied by D. MacLean (pers. comm.; University of New Brunswick): 1184 second-instar larvae per 10 m^2 = 24 second-instar larvae per branch, giving a conversion rate of 24/1184 = 0.0203. This makes the Ostaff and MacLean (1989) conversion: 1570 third-instar larvae per m^2 x 10 = 15700 third-instar larvae per 10 m^2

15700 x 0.0203 = **318.71 third-instar larvae per branch**

(Conversion rate based on data reported by SOPFIM, Société de protection des forêts contre les insectes et maladies, Quebec)

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